

# SPATIAL AND TEMPORAL VARIATIONS IN THE CONDITION OF *AUSTROVENUS STUTCHBURYI* FINLAY, 1927 (BIVALVIA: VENERIDAE) FROM THE AVON-HEATHCOTE ESTUARY, CHRISTCHURCH

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## ABSTRACT

Marsden, I.D. & Pilkington, R.M. (1995). Spatial and temporal variations in the condition of *Austrovenus stutchburyi* Finlay, 1927 (Bivalvia: Veneridae) from the Avon-Heathcote Estuary, Christchurch. *New Zealand Natural Sciences* 22: 57-67.

Weight relationships of the cockle *Austrovenus stutchburyi* were investigated from 9 low tide sites within the Avon-Heathcote estuary in December 1990. The condition index varied significantly between sites. Mean condition index increased with both higher salinity and increased chlorophyll *a* levels, measured during low tide periods. Results from a 15 month sampling programme showed seasonal patterns in the condition index and dry tissue weights of cockles collected from a marine and a more estuarine site. Highest values were recorded in Spring and lowest values in January and February. Cockles from the more estuarine site showed delayed onset of weight gain and a smaller maximal size than those from the marine site. It is suggested that estuarine cockles show reduced reproductive potential and reduced growth rates compared with the more marine population. The role of reduced salinity as a limiting factor affecting growth in cockles is discussed.

Keywords: *Austrovenus stutchburyi* - dry weight - condition index - bivalve growth - reproduction.

## INTRODUCTION

The New Zealand cockle *Austrovenus stutchburyi* is a dominant bivalve of the intertidal community in estuaries and sheltered bays. Some ecological studies have described its distribution patterns and growth rates from different parts of New Zealand (Larcombe 1971, Stephenson 1981, Blackwell 1984, Dobbinson *et al.* 1989, McArdle & Blackwell 1989). However, there have been no previous studies investigating the effects of salinity on the ecology or growth of the cockle. Many factors are known to affect the growth rates of bivalves (Bayne 1976) with commercial species such as mussels and oysters receiving the most attention (Buxton *et al.* 1981, Brown 1988). Although fewer studies have investigated growth and reproduction of clams, the major factors thought to affect growth include: body size; temperature; tidal level; emersion time; density, salinity and food availability (Seed & Brown 1975, Broom 1982, Bayne & Newell, 1983, Beukema *et al.* 1985, Fritz 1991). Bivalves

that inhabit estuaries are not only exposed to tidal variables and a fluctuating salinity regime, but may also be exposed to heavy metals and other pollutants that are known to affect growth and reproduction (Vernberg 1976, Widdows 1985, Marcus *et al.* 1989, Widdows *et al.* 1990, Roper *et al.* 1991).

In a previous study on cockles in the Avon-Heathcote estuary, Stephenson (1981) investigated the weight relationships of cockles from 200 stations in the estuary. Results suggested considerable variation in growth rate and annual production within the estuary. While substratum type and tidal level appeared to explain much of the variability in growth rates, cockle density or biomass were not correlated with any particular environmental factor. However salinity measurements were not recorded as part of that study.

The present study was designed to investigate the weight relationships of cockles exposed to low tide salinities between 13 and 34 ppt. The health of cockles was assessed by a condition index (Crosby & Gale 1990). The sites were restricted to those of

intermediate cockle density (200 to 500 individuals  $m^{-2}$ ; Stephenson 1981). They were located at the low tide level and consisted of similar sediment characteristics (MacPherson 1978). The study examines the variability in the weight relationships within and between localities in the estuary and compares the seasonal weight changes at two localities, one with a high and the other with a low salinity regime.

## MATERIALS AND METHODS

Individuals of *A. stutchburyi*, were collected from 9 sites during December 1990. The sites were chosen along an environmental gradient from less saline areas close to the two river mouths, to fully saline conditions close to the estuary mouth (Fig. 1). The bivalves were collected at high tide by a SCUBA diver sampling at low tide level (approximately 0.2 m above chart datum). Preliminary sampling showed that cockle densities at these locations were below 500  $m^{-2}$  (see also Stephenson 1981). For each site, 30 bivalves of a representative size range were used for weight relationships. Shell length, the maximum distance between the anterior and posterior margins of the shell, was measured to the nearest 0.1 mm using vernier calipers.

The condition index (CI) dry tissue weight/shell weight  $\times 100$  was chosen because this index has been shown previously to correspond with increases in somatic and reproductive tissues, in other bivalves. It can also be measured with precision (Crosby & Gale 1990, Pridmore *et al.* 1990, Rainer & Mann 1992). Surface water temperature ( $^{\circ}C$ ) was recorded at the time of cockle collection and water samples (3 replicates) were taken through a 0.1 mm plankton net, from the surface water and water from the sediment surface. Chlorophyll *a* levels were estimated using a Turner fluorimeter calibrated using known concentrations of chlorophyll *a* ( $\mu g l^{-1}$ ) standards (Yentsch & Menzel 1963). At each site, salinity measurements (ppt) were recorded using a hand held refractometer, during both high and low tide periods.

The two sites selected for a temporal study were an estuarine site close to the Heathcote River mouth (Site 2) and a more saline marine site close to Beachville Road (Site 9). Monthly samples of cockles were taken at spring tides from November 1990 to February 1992. Unfortunately, the cockle samples collected during March 1991 were lost. At both sites,

samples were collected using up to 10 random quadrats (0.25  $m^2$ ) and 30 individuals chosen randomly representing the size range available. For each sample, mean CI was calculated together with the SD and coefficient of variation. The effect of cockle size on the weight relationships was investigated by regression analysis of shell length and dry tissue weights. Comparisons between sites and between different time intervals were made first by testing for heterogeneity of the data followed by analyses of covariance (Snedecor & Cochran 1960). At each site, the environmental variables described earlier were recorded at each time interval and in addition, a salinity profile was undertaken at three-monthly intervals from the time of low tide through to high tide.

Age structure of *A. stutchburyi* from the two sites was compared by counting the annual shell growth rings using the techniques described in Stephenson 1981. Larcome (1971) and Coutts (1974) have confirmed the formation of annual rings in populations of cockles from southern New Zealand. Not all individuals showed clear external annual rings but confirmation of a winter ring was seen at both sites between July and August of the monthly sampling programme. One hundred individuals from each site were collected between November 1991 and February 1992. Shell length, dry weight and number of rings were recorded for each individual. Length-age plots were constructed for cockles collected from both sites and the mean age calculated for each 2.5 mm length group. The density of cockles from the study areas had remained similar over this time with a mean density  $\pm$  SE of  $357 \pm 37.6 m^{-2}$  at the estuarine site and  $279 \pm 31.3 m^{-2}$  at the more saline marine site.

## RESULTS

Mean condition indices for cockles collected at different sites in the estuary are shown in Table 1. No cockles were found at Site 8 which is a region of strong water currents close to the mouth of the estuary. The highest individual condition index, 9, and highest mean condition index, 7, were found in front of the oxidation pond (Site 3). The lowest indices were from Beachville Road (Site 9). The condition index varied significantly between sites (ANOVA  $F_{[7,228]} = 29.3$ ,  $P = 0.001$ ) and there was a high degree of within site variation along the eastern

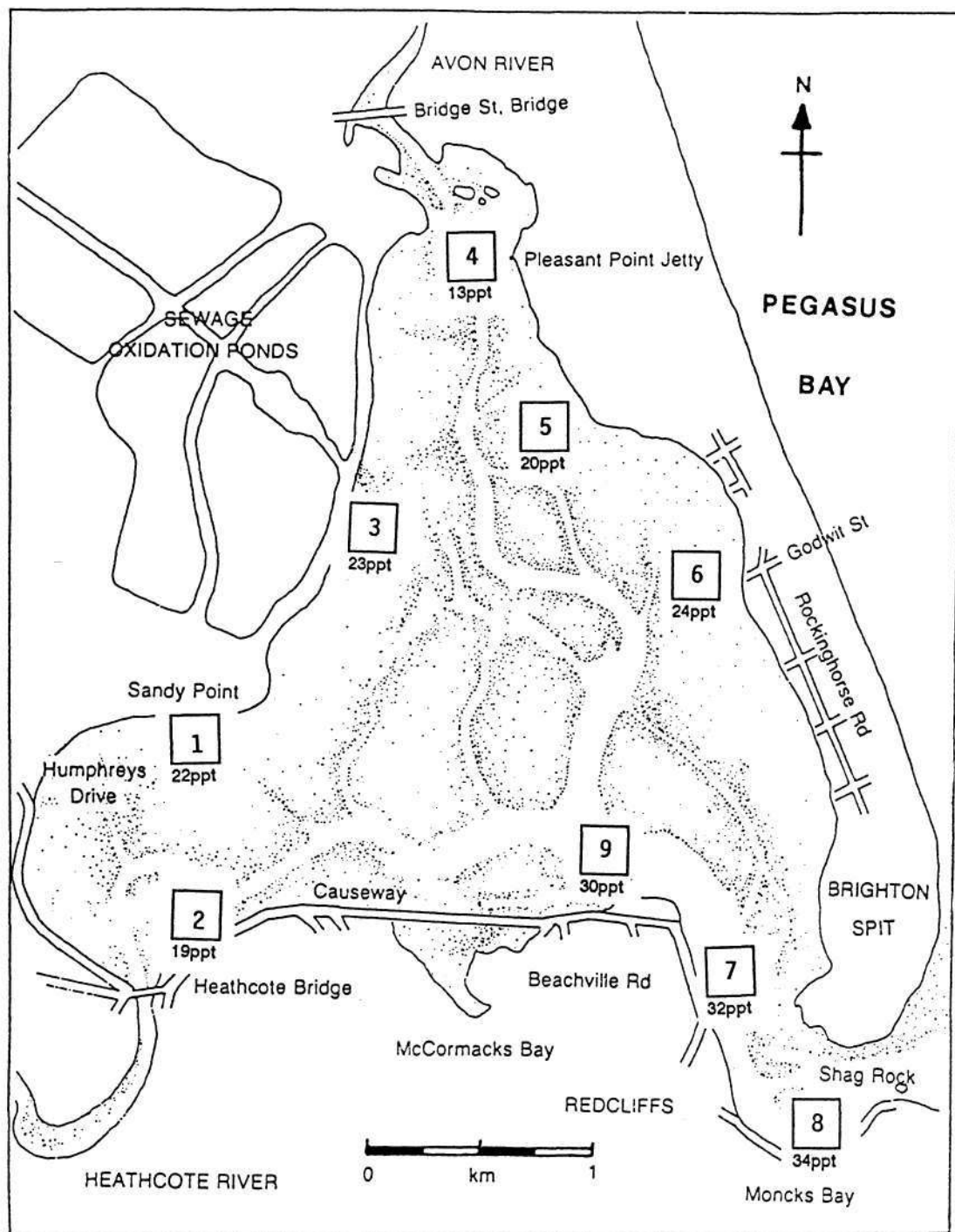


Figure 1. Location of sampling sites in the Avon-Heathcote Estuary and low tide salinity values (ppt). 1. Humphries Drive; 2. Heathcote River Mouth; 3. Oxidation ponds; 4. Avon River mouth; 5. Jellicoe Park; 6. Heron Street; 7. Estuary Channel; 8. Moncks Bay; 9. Beachville Road.

Table 1. Mean condition index (CI) of *A. stutchburyi* within the Avon-Heathcote estuary and chlorophyll *a* levels ( $\mu\text{g l}^{-1}$ ). SD, standard deviation; CV, coefficient of variation corrected for bias.

| Site | Mean | SD   | CV   | Chlorophyll <i>a</i> ( $\mu\text{g l}^{-1}$ ) |         |
|------|------|------|------|---|---------|
|      |      |      |      | surface                                       | benthic |
| 1    | 5.14 | 0.90 | 17.6 | 5.3   | 5.0     |
| 2    | 4.33 | 0.77 | 18.0 | 3.7   | 3.0     |
| 3    | 7.07 | 1.27 | 18.2 | 7.1   | 6.8     |
| 4    | 4.21 | 0.98 | 23.3 | 4.8   | 4.1     |
| 5    | 4.32 | 0.89 | 20.9 | 4.1   | 5.3     |
| 6    | 4.37 | 1.06 | 24.6 | 3.0   | 3.0     |
| 7    | 4.65 | 1.34 | 29.0 | 4.4   | 5.3     |
| 9    | 4.12 | 0.84 | 18.2 | 3.7   | 3.0     |

margin of the estuary. Multiple comparison tests (Newman Keuls) comparing mean condition indices between sites, separated out Site 3 (oxidation ponds); grouped sites 1 (Humphries Drive) and 7 (estuary channel), but found no significant differences between the remaining sites ( $P < 0.05$ ).

At all sites, cockle tissue dry weight ( $y$ ) increased significantly with shell length ( $x$ ) following the equation  $y = ax^b$ . The regression lines were all significant ( $P < 0.001$ ), and Table 2 shows the regression parameters and the predicted dry tissue weight for a standard cockle of length 25 mm. This length was chosen as individuals of this size occur throughout the Estuary. Cockles of the standard size collected close to the oxidation ponds (Site 3) were twice the tissue weight of cockles from Humphries Drive (Site 1).

Tissue weight relationships of cockles from adjacent sites were compared, firstly by testing for heterogeneity of the data. If the data were homoge-

enous then the regression lines were tested for differences in the slope or elevation of the lines. Differences in the elevation of the regression lines were considered only if the slope values were similar. These comparisons are shown in full in Table 3. They show significant differences between sites, either due to heterogeneity of the data (Sites 9 & 2), differences in slope values (Sites 1, 3, 4, 5) or elevation (Sites 1 & 2, 5 & 6, 6 & 7). However, dry weight relationships of cockles from more saline regions, Beachville Road and the estuary channel (Sites 7 & 9) were similar.

A comparison of the shell weight relationships showed a consistent increase in shell weight with shell length. The overall mean slope value (3.8) is similar to that relating dry tissue weight to shell length (3.3). This suggests that for cockles from the estuary, shell weight and tissue weight increase similarly with increasing body length. There was less variation in shell weight than dry tissue weight

Table 2. Weight relationship of *A. stutchburyi*. Values for  $a$  (intercept) and  $b$  (slope) from regression equations  $y = ax^b$  relating dry tissue weight to shell length (Tissue) and shell weight to shell length (Shell) from 8 sites. Also shown are the estimated tissue weights (g) and shell weight (g) of a standard cockle of 25 mm length calculated from the regression lines.

| Site | Tissue |      | Wt. 25mm<br>cockle | Shell  |      | Wt. 25mm<br>cockle |
|------|--------|------|--------------------|--------|------|--------------------|
|      | $a$    | $b$  |                    | $a$    | $b$  |                    |
| 1    | -14.63 | 3.85 | 0.10               | -11.42 | 3.78 | 2.14               |
| 2    | -13.17 | 3.45 | 0.13               | -11.58 | 3.88 | 2.48               |
| 3    | -14.39 | 3.97 | 0.21               | -10.08 | 3.45 | 2.83               |
| 4    | -10.73 | 2.65 | 0.11               | -10.34 | 3.50 | 2.56               |
| 5    | -11.82 | 2.98 | 0.11               | -9.77  | 3.35 | 2.74               |
| 6    | -11.99 | 3.05 | 0.11               | -14.06 | 4.67 | 2.64               |
| 7    | -11.30 | 2.93 | 0.16               | -10.68 | 3.61 | 2.54               |
| 9    | -12.20 | 3.18 | 0.14               | -11.96 | 3.99 | 2.40               |

Table 3. Comparison of the dry tissue weight/length relationships of *A. stutchburyi* between sites. F values for homogeneity and analysis of covariance (ANCOVA) F values testing for differences in slope and intercept values; d.f. degrees of freedom; \*, significant at  $P = 0.005$ ; \*\*, significant at  $P = 0.001$ .

| Lines tested | F-Homogeneity |       | F-Slope |      | F-Constant |      |
|--------------|---------------|-------|---------|------|------------|------|
|              | F-value       | d.f.  | F-value | d.f. | F-value    | d.f. |
| 1 & 2        | 2.15          | 28,28 | 0.66    | 1,56 | 7.20**     | 1,57 |
| 1 & 3        | 1.13          | 24,28 | 8.76**  | 1,52 | 30.55**    | 1,53 |
| 3 & 4        | 1.35          | 24,28 | 17.48** | 1,52 | 16.17**    | 1,53 |
| 4 & 5        | 1.01          | 28,28 | 8.19**  | 1,56 | 0.58       | 1,57 |
| 5 & 6        | 1.63          | 28,28 | 0.43    | 1,56 | 4.28*      | 1,57 |
| 6 & 7        | 1.75          | 28,28 | 2.30    | 1,56 | 41.88**    | 1,57 |
| 7 & 9        | 1.69          | 28,28 | 0.15    | 1,56 | 0.45       | 1,57 |
| 9 & 2        | 4.00**        | 28,28 | 0.70    | 1,56 | 13.69**    | 1,57 |

of cockles between sites, and for the standard length cockle (25 mm), the heaviest shells were found in the vicinity of the oxidation ponds (Table 2).

At the time of sampling, temperatures were similar between sites within the estuary but chlorophyll *a* levels differed for surface and benthic water samples (Table 1). Low tide salinity values (Fig. 1) ranged from 13 ppt, close to the mouth of the Avon River to 34 ppt at the estuary mouth. This salinity gradient is consistent with the increasing distance from the mouth of the estuary at Shag Rock. Regression analyses indicated a significant correlation

between mean condition index for cockles at the 8 sites with both salinity ( $r^2 = 0.89$ ) and chlorophyll *a* concentration ( $r^2 = 0.74$ ).

Temporal effects on the condition index of *A. stutchburyi* are shown in Figure 2 for cockles collected monthly from the marine (Site 9) and a more estuarine location (Site 2). For both sites there were significant seasonal differences in the weight parameters that make up the condition index. At any particular time the variation in CI was greater between sites than within sites. A cyclic pattern was evident in both populations but this was greater in

Table 4. Comparison of weight relationships in *A. stutchburyi* from estuarine and marine sites. Parameters *a* and *b* are from the regression lines relating dry tissue weight (g) to shell length (mm). Also shown are results of tests for homogeneity ( $df = 28,28$ ) and ANCOVA F slope ( $df = 1,56$ ) and F intercept ( $df = 1,57$ ) \*, significant, at  $P < 0.05$ , \*\*, significant at  $P < 0.001$ .

| Month     | Estuarine Site |      | Marine Site |      | F-Homogeneity | F-Slope | F-intercept |
|-----------|----------------|------|-------------|------|---------------|---------|-------------|
|           | a              | b    | a           | b    |               |         |             |
| November  | -11.10         | 2.79 | -12.14      | 3.20 | 1.06          | 1.95    | 63.82**     |
| December  | -13.17         | 3.45 | -12.20      | 3.18 | 4.00**        | 0.70    | 13.69**     |
| January   | -11.50         | 2.91 | -12.46      | 3.22 | 1.39          | 0.01    | 13.93**     |
| February  | -12.21         | 3.12 | -12.44      | 3.23 | 1.44          | 0.002   | 14.70**     |
| April     | -12.10         | 3.09 | -10.68      | 2.73 | 1.23          | 7.79**  | 55.85**     |
| May       | -11.71         | 2.98 | -13.06      | 3.42 | 24.13**       | 0.19    | 0.91        |
| June      | -12.31         | 3.14 | -12.33      | 3.23 | 1.29          | 1.24    | 31.89**     |
| July      | -13.52         | 3.52 | -11.83      | 3.09 | 1.45          | 0.002   | 27.69**     |
| August    | -14.45         | 3.85 | -12.23      | 3.23 | 1.02          | 0.50    | 26.23**     |
| September | -12.53         | 3.25 | -12.47      | 3.32 | 1.57          | 2.84    | 39.09**     |
| October   | -11.79         | 3.03 | -13.89      | 3.74 | 1.67          | 19.60** | 25.20**     |
| November  | -11.93         | 3.06 | -12.80      | 3.37 | 3.66**        | 0.88    | 20.85**     |
| December  | -13.91         | 3.64 | -9.16       | 2.38 | 2.46*         | 14.05** | 76.48**     |
| January   | -12.35         | 3.14 | -12.12      | 3.16 | 1.14          | 3.59    | 84.99**     |
| February  | -12.28         | 3.13 | -12.39      | 3.25 | 216.6**       | 0.01    | 0.002       |



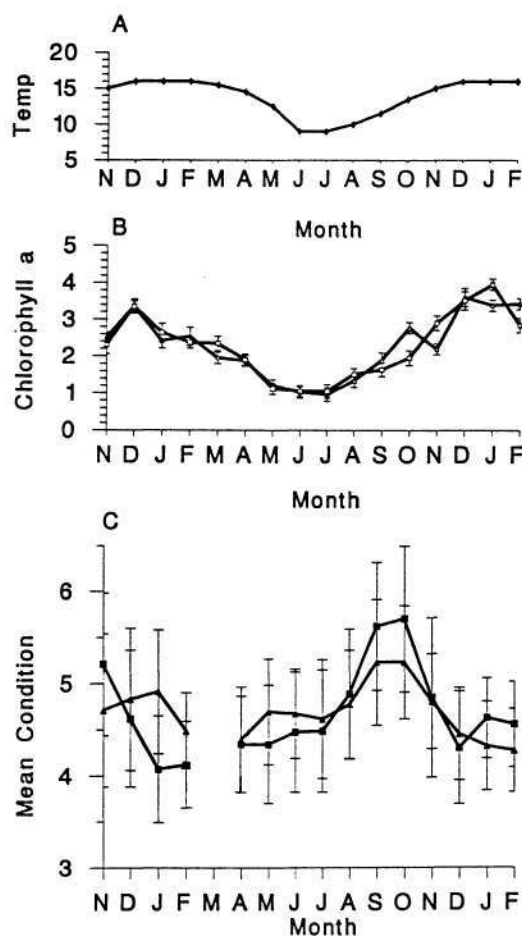


Figure 2. Temporal variation in A, low tide seawater temperatures, °C (circles); B, mean chlorophyll *a* concentrations, for estuarine Site 2 (open triangles) and for marine Site 9 (open squares) and C, the mean condition index ( $\pm$  SE) of *Austrovenus stutchburyi* at the estuarine site (closed triangles) and at the marine site (closed squares) within the Avon-Heathcote Estuary.

cockles from the more marine site than the estuarine site. Highest CI values were found at both sites during the spring (September and October) with lowest overall values in January 1992, at the marine site and February 1993, at the less saline site. Low tide seawater temperatures were similar at both locations throughout the year with a temperature of approximately 8°C during winter (June and July) and 16°C in the summer (December to February). Over the year, cockle condition index did not correlate directly with either seawater temperature or chlorophyll *a* measurement at either location

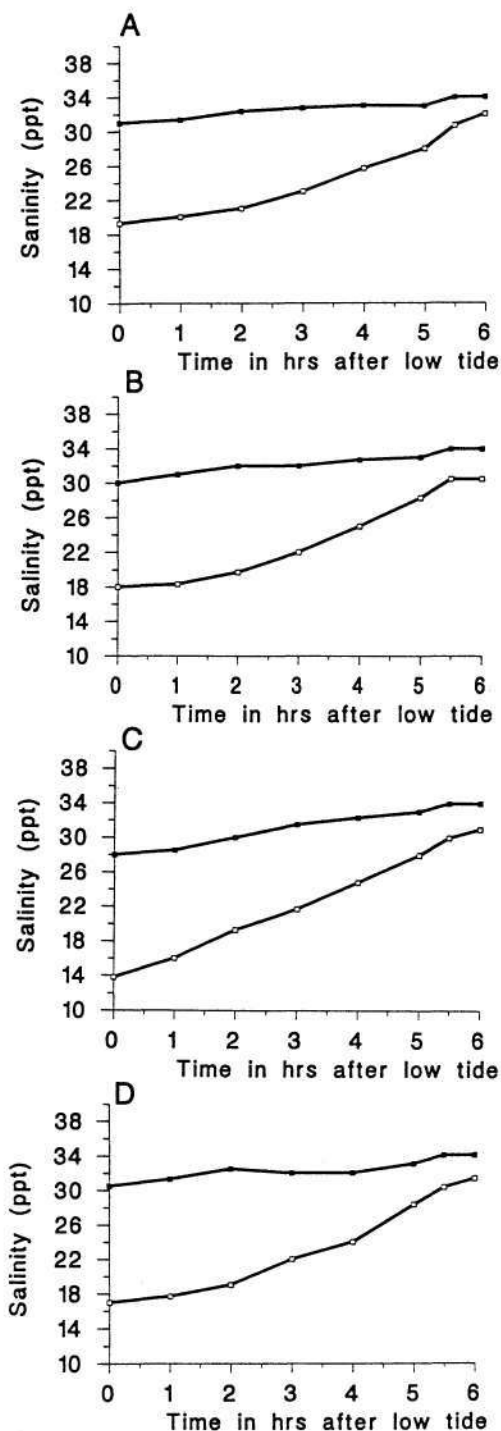


Figure 3. Tidal salinity profiles for the estuarine (open squares) and marine site (closed squares) recorded in A Summer; B Autumn; C Winter and D Spring. Values are mean of 5 values, time 0 is the time of low tide.

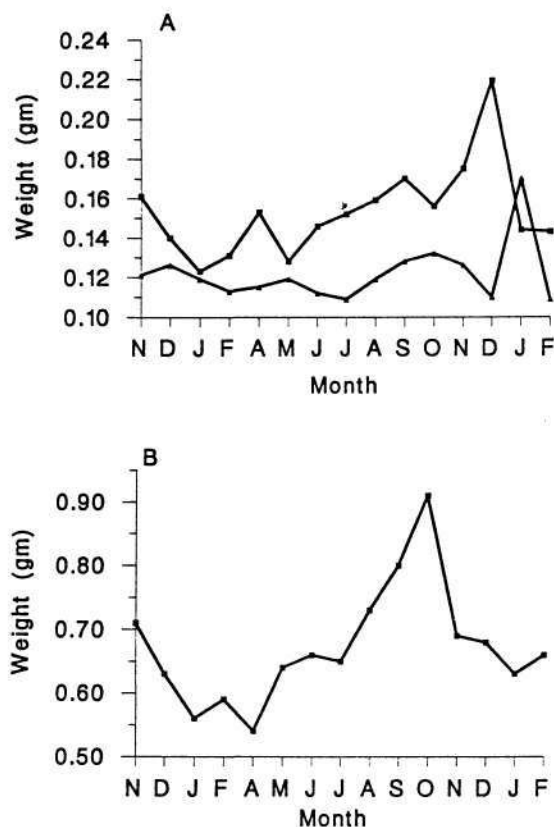


Figure 4. Seasonal variations in the estimated dry tissue weight of *A. stutchburyi*, A, 25 mm length from the estuarine (triangles) and marine (squares) sites. Also shown B, is the estimated weight of a 40 mm length cockle (squares) from the marine site.

(Fig. 2). However, chlorophyll *a* levels followed the seasonal temperature profile with maximal values during December or January. The salinity regime at each site was consistent throughout the year (Fig. 3) but tidal fluctuations differed between 13.5 ppt and 35 ppt at the estuarine site (5 ppt h<sup>-1</sup>) and between 30 ppt and 34 ppt (<0.7 ppt h<sup>-1</sup>) at the marine site.

The condition index (CI) was independent of body size within the length range of cockles examined in the present study. Regression equations relating dry tissue weight to shell weight resulted in slope values close to 1.0 for both populations suggesting similar increases in tissue weight with increasing shell weight. In 10 out of the 15 seasonal samples marine cockles showed a higher CI than the more estuarine cockles.

Although the maximal length of cockles col-

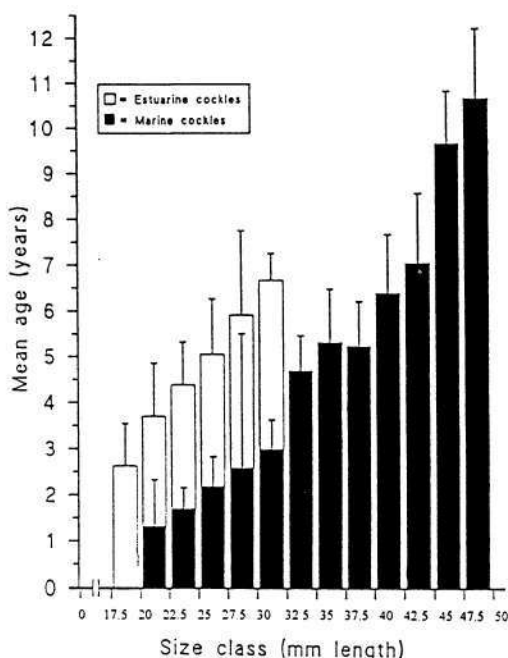


Figure 5. Estimated age/size relationships (+ SE) of *A. stutchburyi* from estuarine and marine sites.

lected from the estuarine site (31 mm) was less than that from the marine site (48 mm), regression lines relating dry tissue weight to shell length had similar slope values at both locations (Table 4). The mean slope value for cockles from the marine site was 3.8 compared with 3.2 from the more estuarine site. The larger size of many cockles from the marine site resulted in significant heterogeneity of some of the monthly samples, invalidating comparison of regression lines by ANCOVA. Each month there were significant differences in the dry weight length relationship of cockles from the two areas.

Figure 4 shows seasonal variation in the estimated dry tissue weight for a cockle of 25 mm length from both sites and also the weight for 40 mm length cockles from the marine site. Forty millimetre length cockles from the marine site were at their winter minimal tissue weight in April, then increased to maximal values in October when gonad weight (estimated by difference from the minimal value after spawning) constituted 42% of the body weight. Smaller cockles from the marine site also showed weight gain over the winter. This feature was not shared by the estuarine population, where the onset of weight increase was delayed by two months.

These results suggest a delayed breeding and spawning period in the estuarine population. Prior to the first spawning event of the annual breeding cycle the projected weight increase due to gametogenesis was 78% in the marine cockles compared with 23% for those cockles exposed to more estuarine conditions.

Growth rates in bivalves can be represented by increases in tissue weight, which is variable depending on the stage in the reproductive cycle, or by changes in shell weight or dimensions. During the temporal study, a new shell growth ring was evident externally between mid July and mid August in 30 to 50% of individuals from both populations. Length-age plots, constructed for cockles from both sites suggested marked differences in the age distribution and growth rates at the two sites. Comparison of the mean ages of length groups (Fig. 5), suggests that over the first 4 years, marine cockles reach 32 mm shell length compared with 23 mm for the estuarine group. The largest cockles (40–49 mm length) were collected from the marine site and were estimated to be approximately 11 years old. In contrast the largest estuarine cockles were approximately 30 mm shell length and estimated to be 9 years old.

## DISCUSSION

The cockle *Austrovenus stutchburyi* shows both spatial and seasonal variations in weight relationships within the Avon-Heathcote estuary. The estuary survey detected variation in the condition index that was related to both salinity and chlorophyll *a* levels, consistent with known nutrient levels. The Avon-Heathcote is a shallow estuary that receives nutrient inputs from the two rivers and the oxidation ponds. Close to the oxidation ponds (Site 3) there were low salinity values and a high condition index for *A. stutchburyi* consistent with high nutrient levels. Stephenson (1981) estimated that the oxidation ponds provide major nutrient input supplying 94% of the phosphorus and 80% of the total nitrogen available in the estuary.

The condition index values for cockles from the present study were also related to salinity reduction due to fresh water inputs from the rivers. The lowest values were recorded from the low salinity region close to Avon River mouth (Site 4) which is above the site of discharge from the oxidation ponds and an area that receives low levels of nutrient input.

Many factors are thought to affect the condition

indices of bivalves including population density, size, gonad development, height on the shore, nature of the substratum, salinity, temperature, food supply, fouling and pathogens (Lucas & Beninger 1985, Muniz *et al.* 1986, Marcus *et al.* 1989, Crosby & Gale 1990, Pridmore *et al.* 1990, Fritz 1991, Littlewood *et al.* 1992, Rainer & Mann 1992). The condition index response to environmental change is often species specific and may differ for example within bivalve groups, such as oysters and also between environmental contaminants (Frazier 1976, Pridmore *et al.* 1990).

For *A. stutchburyi*, the condition index has been shown to be affected by tidal height and immersion time (Dobbinson *et al.* 1989), but was not effective in distinguishing between cockles from polluted and unpolluted sites in the Manukau Harbour, New Zealand (Gardner 1992). Some other studies have found a negative correlation between condition index and size in molluscs (Hickman & Illingworth 1980, Ansell *et al.* 1984), but this was not consistent for *A. stutchburyi*. The condition index would be expected to vary with size if, during growth, the shell weight increased markedly with shell size due to increased shell thickness. Within the Avon-Heathcote estuary the shell weight characteristics of the cockle were similar from all sites suggesting that changes in the condition index represent variations in the weight of somatic and gonad tissue. This allows the condition index to be a useful tool in comparing cockles from different localities.

The seasonal changes in tissue dry weight recorded for *A. stutchburyi* from two sites differing in their salinity regime largely reflect stages in the reproductive cycle (see also Larcombe 1971). For the European cockle *Cerastoderma edule* as in *A. stutchburyi* the timing of gametogenesis is known to vary both between localities and between years with some populations starting gametogenesis in the autumn whilst others report initiation later in the winter (Seed & Brown 1975, Newell & Bayne 1980, Ivell 1981, Navarro *et al.* 1989). While temperature differences may explain spatial differences in some cases, in the present study, the two subpopulations of cockles were exposed to relatively similar thermal regime and nutrient levels.

Variability in the reproductive cycles of bivalves has been reported previously for bivalves (Kautsky 1982, Thompson & Nichols 1988, Heffernan *et al.* 1989a,b, Hesselman *et al.* 1989) including mussels



(Newell *et al.* 1982), where it is related to fluctuations in the storage cycle as a result of food availability and accumulation of carbohydrate reserves. Similarly, in the cockle *C. edule*, gametogenesis is thought to occur earlier if the glycogen stores depleted during spawning are able to be replenished (Navarro *et al.* 1989, Iglesias & Navarro 1991). In the present study while differences in nutrient levels between sites cannot be discounted, the major environmental variable that differed between the two populations was salinity. The cockles from the less saline regime showed delayed weight gain and lower maximal body tissue weight may indicate reduced reproductive potential. The effects of salinity on the reproduction of bivalves is not well understood. However, reduced salinity is known to retard growth in mussels (Gruffydd *et al.* 1984, Navarro 1988) and the European cockle *C. edule* (Kristensen 1956). It is also thought to act as a stimulus for spawning in the Pacific oyster (Arakawa 1990). The estimated annual length increase in cockles from the almost fully marine habitat in the Avon Heathcote estuary is similar to that recorded by Dobbinson *et al.* 1989 for high shore cockles transplanted to low shore cages in Otago Harbour (salinity 31.5 to 34.8 ppt). Our study however suggests that cockles from low salinity areas may have reduced growth rates.

Although many studies have investigated the effects of reduced salinity on the physiology of marine organisms, the responses have been variable (Lockwood 1976, Newell 1979). Some invertebrates acclimate to changing salinities while in others salinity can act as an environmental stressor. The New Zealand cockle, unlike many other low tide bivalves, shows regular circatidal rhythmicity in shell opening behaviour with maximal activity during the 3 hours associated with the high tide period (Beentjes & Williams 1986, Williams *et al.* 1993). Laboratory exposure of cockles to low salinity conditions shows that the onset of feeding can be delayed or an activity period can be missed (Pilkington 1992). If this inhibition of feeding occurs in field populations, then the effects of low salinity on growth and reproduction suggested in this study may be a direct consequence of environmental stress and/or reduced energy acquisition.

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